Symbionts of the hermit crab *Pagurus longicarpus* Say, 1817 (Decapoda: Anomura): New observations from New Jersey waters and a review of all known relationships

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Abstract.—The gastropod shell-*Pagurus longicarpus* complex harbors a variety of associates representing different kinds of symbiosis. There are 31 known relationships, 24 of which have been found with hermit crabs from New Jersey, U.S.A. These involve species from eight phyla, living on, embedded in, or in the lumen of the gastropod shells, as well as on or in the crab host. Crabs primarily inhabited the shells of *Nassarius obsoletus* (75.7%; *n* = 6757). The hydroid *Hydractinia symbiolongicarpus* and the bryozoan *Alcyonidium albescens* dominated the outside surfaces of shells (51.5% and 26.5%, respectively), and a predatory relationship between the bryozoan and the nudibranch *Corambe obscura* was observed. *Dipolydora commensalis* and *Lepidonotus sublevis* were the most common polychaetes living in shell burrows (38.9%) and in the shell lumen (25.8%), respectively. Acrothoracican barnacles, *Trypetesa lampas,* were embedded in 4.7% of shells. In New Jersey *P. longicarpus* is parasitized by the isopods *Stegophryxus hyptius* and *Paguritherium alatum.* Among known parasites of the crab not yet recorded from New Jersey are the isopod *Asymmetrione desultor,* plerocercoid larvae of the cestode *Calliobothrium verticillatum,* and cystacanth larvae of the acanthocephalan *Polymorphus* sp.

The longwrist hermit crab *Pagurus longicarpus* Say, 1817, resides in Atlantic coastal waters of the United States from Maine to the Gulf of Mexico (Williams 1984). In the mid-Atlantic region crabs are abundant intertidally in depressions on exposed muddy sand flats during the warmer months, but retreat to the subtidal for the winter (Rebach 1974, 1978; McDermott, pers. obs.). Many aspects of the crab's biology have been studied, including feeding, shell acquisition, environmental tolerances, reproduction, and symbiotic relationships (see McDermott 1999). The term *symbiosis* is used in the original and general way referring to "the living together of unlike organisms" (Committee on Terminology 1937).

Pagurus longicarpus harbors a variety of symbionts, which are attached to the outside or inside of occupied gastropod shells, burrowed into the shell, or free in the shell's lumen, and the crab itself is host to several species of ecto and endosymbionts. Some of the symbionts are specific for this hermit crab, while others, although showing predilections for the crab, are found often on a variety of other surfaces. Thus, *P. longicarpus* with its molluscan shell serves as host for a diversity of organisms from protozoans to crustaceans.

The present paper documents the species of gastropod shells utilized by *P. longicarpus* and symbionts associated with the shells and the crabs themselves from the waters of New Jersey. This is followed by a review of the biology of all known symbiotic relationships. As stated so colorfully by Allee (1923), "*Pagurus longicarpus* apparently roams at will . . . carrying with him, willy-nilly his commensals."

Materials and Methods

An intertidal population of *Pagurus longicarpus* located in Hereford Inlet estuary (Grassy Sound Channel 39°01.72′N, 74°48.10′W) has been under study since the mid-1960's (Biggs & McDermott 1973, Lytwyn & McDermott 1976, McDermott 1998, 1999). Water temperatures range from 1° to >25°C, and mean salinity is ~30‰. Crabs were collected randomly by hand on exposed tidal flats from 1986 to 1990. They were isolated in the field in compartmentalized, plastic boxes containing sea water (each of 18 compartments were 51 × 43 × 39 mm), or were immediately preserved in bulk in 10% sea water-Formalin and later transferred to 70% ethyl alcohol. The gastropod shells harboring hermit crabs were identified, and their lengths were measured with Vernier calipers to 0.1 mm. External symbionts on these shells were identified, and those that could be removed (e.g., nudibranchs or calyptraeid gastropods) were preserved for later study. Shells were then cracked with a hammer, crabs were isolated in fresh sea water, and symbionts embedded in the shell fragments or found in the lumen were identified. Isolated crabs were sexed and the length of the anterior shield of the carapace (SL) was measured with Vernier calipers to 0.05 mm. Preserved crabs were treated in a similar manner; however, the prevalence of animals not cemented to the shells (e.g., nudibranchs from the outside of the gastropod shells, and polyclad turbellarians, polychaetes and calyptraeid gastropods from the lumen) could not be determined from the preserved collections. Observations on reproduction were made on some of these symbionts. The prevalence of epicaridean isopod parasites was determined from live and preserved crabs as described in McDermott (1998), although crabs were not routinely dissected to look for other internal parasites.

Results

Of the 6757 shells inhabited by *Pagurus longicarpus,* 95.0% were *Nassarius obsoletus* (Say) and *N. trivittatus* (Say), 75.7% and 19.3%, respectively (Table 1). Crabs occupied 137 shells of *Urosalpinx cinerea* (Say) (2.0%), and the other 13 gastropod species made up only 3.0%.

A partially annotated list of all symbionts found within the host shell-*Pagurus longicarpus* complex in this study, as well as all other known symbionts, appears in Table 2.

There were 20 species of invertebrates associated with shells harboring *P. longicarpus* from the live and preserved crab collections from New Jersey waters (Table 3; $n = 5041$). The hydroid *Hydractinia symbiolongicarpus* and the ctenostome bryozoan *Alcyonidium albescens* were the dominant species encrusting outside surfaces of hermit shells, while the polynoid polychaete *Lepidonotus sublevis* was the main inhabitant of the shell lumen. The two calyptraeid gastropods *Crepidula convexa* and *C. plana,* found on the outside and inside of the shell, respectively, were equally prevalent. Spat of the blue mussel *Mytilus edulis* was attached to the outside and inside of the shell and the exoskeleton of the crab predominately from January to April.

A prey-predator relationship exists between the bryozoan *Alcyonidium albescens* and the nudibranch *Corambe obscura.* The bryozoan was attached to 701 of the 2838 (24.7%) shells, while the nudibranch and/or its coiled egg strings were found on 78 (2.8%) shells. Three of these shells were without the snail itself, but since its egg strings were present, it was assumed that at least one nudibranch from each shell had been dislodged when the crabs were collected. Except for three shells which lacked *A. albescens, C. obscura* was otherwise found only on shells harboring the bryozoan (96.2%). Only three of the 2137 shells *without A. albescens* (0.14%) had the nudibranch, while 75 of the 701 shells *with* the bryozoan (10.7%) harbored the preda-

Table 1.—Gastropod shells inhabited by *Pagurus longicarpus* in the Hereford Inlet estuary of New Jersey, based on all collections from 1985 to 1990 (*n* = 6757). Arranged in order of decreasing abundance.*

Species	Number	Percent
Nassarius obsoletus (Say)	5112	75.65
Nassarius trivittatus (Say)	1306	19.33
Urosalpinx cinerea (Say)	137	2.03
Neverita (= *Polinices*) *duplicata* (Say)	59	0.87
Eupleura caudata (Say)	45	0.67
Busycon carica (Gmelin)	23	0.34
Littorina littorea (Linnaeus)	21	0.31
Euspira (= *Lunatia*) *heros* (Say)	19	0.28
Littoraria (= *Littorina*) *irrorata* (Say)	12	0.18
Busycotypus (= *Busycon*) *canaliculatus* (Linnaeus)	9	0.13
Costoanachis (= *Anachis*) *avara* (Say)	7	0.10
Astyris (=*Mitrella*) *lunata* (Say)	3	0.04
Epitonium rupicola (Kurtz)	2	0.03
Littorina obtusata (Linnaeus)	1	0.02
Nassarius vibex (Say)	1	0.02

* Classification based on American Fisheries Society (1998).

tor. Thus, *C. obscura* was 76.4 times more abundant on shells with this bryozoan.

Ninety-nine specimens of *C. obscura* were recorded from 78 shells (1–4/shell), and egg strings were found on 17 shells (1–7/shell). The maximum number of seven strings occurred with a single nudibranch. Observations suggested that there are two periods of reproduction, April–May and September–November. Veligers hatched only from eggs collected in October and November. Mean length of living nudibranchs was 2.41 ± 1.49 mm, range 0.69–4.40 mm (*n* = 14), and snails approximately ≥3.0 mm were mature. One circular egg string measured 2.3 mm in diameter.

The spionid polychaete *Dipolydora commensalis* was the dominant species that bores into the shell, having a prevalence approximately eight times that of the acrothoracican barnacle *Trypetesa lampas*. The prevalence of these symbionts was compared between the two most common host shells, *Nassarius obsoletus* and *N. trivittatus*. *Dipolydora commensalis* occurred in 761 of 2110 (36.1%) of *N. obsoletus* shells and 243 of 570 (42.6%) of *N. trivittatus* shells (significant difference, contingency χ^2 = 8.28, *p* = <0.005). The worm also occurred in shells of six of the other gastropod species listed in Table 1 (31 of 157, 19.8%). Worms were reproducing most of the time that crabs were on the intertidal flats, but no data are available while crabs were subtidal during the winter (December–February). Female worms with mature ova, along with their egg cases in the burrows were seen as early as March, and 3-setiger larvae were hatching in April when the water temperatures during these months ranged from approximately 7° to 12°C. Recently settled juveniles appeared to be most common in the fall. Numbers of worms per shell were usually not counted, but a maximum of eight worms were found in a single burrow, only one of which was a mature female.

Trypetesa lampas was found in 66 of 2110 (3.1%) *N. obsoletus* shells and 9 of 571 (1.6%) *N. trivittatus* shells (significant difference, contingency χ^2 = 4.01, *p* = <0.05). A maximum of four barnacles were found in *N. obsoletus* shells, while no more than one occurred in *N. trivittatus*. Unlike *D. commensalis*, *T. lampas* was not found in 157 of the other shell species. Barnacles with eggs and developing nauplii were observed in August and September of 1987, and liberated nauplii were seen in August 1988.

Epicaridean symbionts on and in the hermit crabs from the same population were studied recently (McDermott 1998) and are listed in Table 2. Their prevalence and biology, along with other crab parasites (Table 3) not yet found in New Jersey waters (Table 2) are discussed below.

Discussion

Crab shell utilization (Table 1).—The species of gastropod shells used by *P. longicarpus* varies over the latter's geographical range. In waters north of New Jersey (Connecticut and Rhode Island) the shells of *Littorina littorea* are used in numbers equal to those of *Nassarius obsoletus* (~25%) (Blackstone & Joslyn 1984), or greatly outnumber the latter by ~80% to <5%) (Scully 1979). The habitat of *N. obsoletus* in New England has gradually contracted due to competitive exclusion since the introduction of *L. littorea* from Europe in the mid-1880's (Brenchley & Carlton 1983). New Jersey is near the southern limit of *L. littorea,* and its populations are relatively small. Shells of the intertidal gastropods *Littorina saxatilis* (Olivi) and *Nucella lapillus* (Linnaeus), species not found in New Jersey, are inhabited infrequently by *P. longicarpus* in Rhode Island (Scully 1979). At Beaufort, North Carolina, where *L. littorea* is rare, *N. obsoletus* and the more southern *N. vibex* are utilized in equal numbers (~30%) (Kellogg 1977). In the same area *Costoanachis avara, Terebra dislocata* (Say) and *Urosalpinx cinerea* are each represented at ~8%. In the North Inlet estuary of South Carolina, Young (1979) found that 56.5% of 1208 *P. longicarpus* were in *Nassarius* spp. shells (he did not distinguish the species, but the majority were probably *N. vibex*). *Terebra dislocata* and *U. cinerea* were each used by ~15% of the crabs. In the northeastern Gulf of Mexico (Florida) *Littoraria irrorata* and *N. vibex* are inhabited by 80% of the *P. longicarpus* population (Kuhlmann 1992). In the Galveston area of the Texas coast, Fotheringham

(1976) recorded 47% of the crabs in shells of *Neverita duplicata* and ~15% each in *L. irrorata* and *Stramonita* (=*Thais*) *haemastoma floridana* (Conrad). *Littoraria irrorata,* the southern periwinkle, is rarely found in New Jersey and northward (Blackstone 1986, McDermott, pers. obs.). In all of the cases mentioned above, it is primarily the shell of the dominant gastropods in the region that are used by *P. longicarpus*. As Fotheringham (1976) and others have noted, shell-use patterns are influenced by a variety of factors including: abundance of shells, shell size, internal volume and shell morphology, crab ontogeny, sex, intra and interspecific competition, and attached symbionts. Besides the 15 gastropod shells in Table 1 and *Terebra dislocata* and *Stramonita haemastoma floridana,* Sumner et al. (1913) noted that *Euspira triseriata* (Say), *E. immaculata* (Totten) and *Colus pygmaeus* (Gould) were also used by *P. longicarpus*. Thus, *P. longicarpus* has been shown to utilize a total of 20 different gastropod species along its range on the east coast.

Symbionts associated with the shell (Tables 2, 3).—The colonial hydroids *Hydractinia symbiolongicarpus* Buss & Yund and *Podocoryne carnea* Sars are both facultative symbionts. The former has recently been recognized as one of three sibling species associated with *P. longicarpus*. It is distinguished from *H. symbiopollicaris* Buss & Yund, *H. polyclina* (Agassiz) and the European *H. echinata* (Fleming) by breeding incompatabilities, electrophoretic analyses, morphometrics, and some specificity for crab hosts (Buss & Yund 1989). *H. symbiolongicarpus* and *H. symbiopollicaris* are found mainly on the shells occupied by *P. longicarpus* and *P. pollicaris* Say, respectively, but the reverse sometimes occurs. Originally *H. polyclina* was found only on shells inhabited by *Pagurus acadianus* Benedict, and not on *P. longicarpus* or *P. pollicaris* (Buss & Yund 1989), but a more recent study has shown that *H. polyclina* may also be found on shells harboring

Table 2.—Master list of symbionts of *Pagurus longicarpus* arranged according to their location in the host shell–hermit crab complex and in phylogenetic order within the location. Most were found in crabs from New Jersey waters.

Symbionts	Remarks*
On Outside of Shell	
Cnidaria	
Hydractinia symbiolongicarpus Buss & Yund	One of three sibling species associated with crabs in genus *Pagurus* (see Discussion)
Podocoryne carnea Sars	Shows a predilection for the shells of *Nassarius trivittatus*
Ectoprocta	
Alcyonidium albescens Winston & Key	Facultative symbiont
Conopium tenuissimum (Canu)	Facultative symbiont
Membranipora tenuis Desor	Facultative symbiont
Schizoporella unicornis (Johnston)	Facultative symbiont
Annelida	
Hydroides dianthus (Verrill)	Facultative symbiont
Sabellaria vulgaris (Verrill)	Facultative symbiont
Mollusca**	
Crepidula convexa Say	Shows some predilection for hermit shells
Crepidula fornicata (Linnaeus)	Seldom with this crab, often on *P. pollicaris*
Cuthona (*nana* ?) (Alder & Hancock)	Predator of *Hydractinia*
Corambe (=*Doridella*) *obscura* (Verrill)	Predator of *Alcyonidium* and other encrusting bryozoans
Mytilus edulis Linnaeus	Seasonal symbiont as spat in breeding seasons (January to April and June)
Arthropoda	
Anoplodactylus (*lentus*) Wilson	Found among the polyps of *Hydractinia*
Balanus eburneus Gould	Facultative symbiont
Balanus improvisus Darwin	Facultative symbiont
Bored into Shell	
Annelida	
Dipolydora (=*Polydora*) *commensalis* (Andrews)	Bores into columella, and may make contact with shell lumen; obligate symbiont
Dipolydora socialis (Schmarda)***	Superficial burrow on outside of shell
Polydora neocaeca Williams and Radashevsky***	Lives in an unbranched U-shaped burrow in hermit shells as well as living gastropods and bivalve shell fragments
Polydora websteri Hartman***	Superficial burrow on outside of shell
Arthropoda	
Trypetesa lampas (Hancock)	Bores from lumen side of body whorl
Lumen of Shell	
Platyhelminthes	
Stylochus zebra (Verrill)	Embryo predator of *P. pollicaris*
Annelida	
Lepidonotus sublevis Verrill	Obligate symbiont
Mollusca	
Crepidula plana Say	Shows predilection for hermit shells
External on Crab	
Protozoa	
Lagenophrys eupagurus Kellicott***	Tests containing peritrichous ciliate attached to gills
Unidentified folluculinid ciliate	Tests containing heterotrichous individuals cemented to body

Table 2.—Continued.

Symbionts	Remarks*
Mollusca	
Mytilus edulis Linnaeus	Seasonal symbiont
Arthropoda	
Asymmetrione desultor Markham***	Bopyrid isopod in branchial chambers
Stegophryxus hyptius Thompson	Bopyrid isopod on abdomem
Internal in Crab	
Platyhelminthes	
Calliobothrium verticillatum (Rudolphi)***	Plerocercoids of tetraphyllidean cestode in *Pagurus pollicaris,* but possibly also in *P. acadianus* and *P. longicarpus*
Acanthocephala	
Polymorphus sp.***	Cystacanths in abdominal hemocoel
Arthropoda	
Paguritherium alatum Reinhard	Entoniscid isopod in hemocoel

* Additional information in Discussion.
** Mollusk classification based on American Fisheries Society (1998).
*** Not identified from New Jersey crabs.

P. longicarpus (Folino & Yund 1998). *Hydractinia* from New Jersey is assumed to be *H. symbiolongicarpus.* The high prevalence of *Hydractinia* on hermit shells (>50%) in New Jersey is consistent with Lytwyn's (1979) observations in the same state in the 1970's. In Texas waters its prevalence was approximately 30% (Fotheringham 1976).

The prevalence of *Podocoryne carnea* on hermit shells from New Jersey was much lower (0.5% of 2838 crabs) than for *H. symbiolongicarpus* (Table 3). McFadden (1986) found that *P. carnea* was rare among the epifauna of *P. longicarpus* shells collected in Long Island Sound. She also noted that recruits of this hydroid were found on only 0.2% of 1663 shells but did not record the species of gastropod shells that harbored *P. carnea.* All 15 colonies of this species from New Jersey crabs were on the shells of *Nassarius trivittatus,* which agrees with Crowell (1945) who showed that *P. carnea* has a predilection for the crab-occupied shells of *N. trivittatus,* almost never being found on the shells of *Littorina littorea,* at least in the Woods Hole

region of Massachusetts. He found both *P. carnea* and *Hydractinia* sp. on crab-occupied shells of *Busycon* sp., *Urosalpinx cinerea, Eupleura caudata, Nassarius obsoletus,* and others. Unlike Crowell, Edwards (1972) identified colonies of *P. carnea* on *Littorina* shells occupied by hermit crabs from the British Isles. *Podocoryne carnea* has free medusae in its life cycle (unlike *Hydractinia*), which are liberated from gonozooids whose white color makes the colony easily recognizable. Gonozooids may be seasonal. Medusae develop and are liberated from late May to early August in colonies on New Jersey crabs. The presence of *P. longicarpus* inside of a *Nassarius trivittatus* shell covered with *P. carnea* in some manner allows for the differentiation of spiral zooids around the periphery of the aperture (Braverman 1960). Although the mechanism involved in this differentiation and the functional significance of this phenomenon have not been explained, it is possible that these elongated zooids may be utilized for capturing food items stirred up from the sediments by the hermit crab or crab zoeae liberated from the shell aperture.

Table 3.—Prevalence of symbionts found on, in, or in the lumen of gastropod shells inhabited by *Pagurus longicarpus* from the Hereford Inlet estuary of New Jersey 1986–1990, based on the examination of shells with live (*n* = 2838) and preserved crabs (*n* = 2203). Species within each phylum are arranged alphabetically.

Species	Live crabs		Preserved crabs	
	Number	Percent	Number	Percent
Cnidaria				
Hydractinia spp.	1475	52.0	1120	50.8
Podocoryne carnea	15	0.5	ND*	
Ectoprocta				
Alcyonidium albescens	701	24.7	634	28.8
Other encrusting species**	35	1.2	76	3.4
Platyhelminthes				
Stylochus zebra	2	0.1	ND	
Annellida				
Dipolydora commensalis	1038	36.6	922	41.9
Hydroides dianthus	10	0.4	6	0.3
Lepidonotus sublevis	612	21.6	688	31.2
Sabellaria vulgaris	90	3.2	47	2.1
Mollusca				
Corambe obscura	78	2.8	ND	
Crepidula convexa	318	11.2	ND	
Crepidula fornicata	2	0.1	ND	
Crepidula plana	320	11.3	ND	
Mytilus edulis spat	213	7.5	ND	
Pycnogonida				
Anoplodactylus (*lentus*)	4	0.1+		
Arthropoda				
Barnacle spat***	34	1.2	ND	
Trypetesa lampas	75	2.6	163	7.4

* ND = no data.
** *Conopium tenuissimum* (Canu), *Membranipora tenuis* Desor, *Schizoporella unicornis* (Johnston).
*** *Balanus eburneus* and *B. improvisus*.
Additional invertebrates that are only loosely associated with shells, primarily in silt accumulated in damaged apices: sea anemone; heteronemerteans, hoplonemerteans; polychaetes, *Polycirrus eximus* (Leidy), *Autolytus* sp., phyllodocids, spionids; amphipods, *Caprella* sp., *Corophium* sp., isopod, *Erichsonella filiformis* (Say); mollusc, *Anadara ovalis* (Bruguière). Living boring sponge *Cliona* sp. was found on one *Nassarius obsoletus* shell.

Pagurus longicarpus and *P. pollicaris* seem to prefer gastropod shells with *Hydractinia* colonies, while some other members of the genus and other genera may reject shells with this hydroid (Conover 1976, Mills 1976, Mercando & Lytle 1980). Other evidence suggests that *P. longicarpus* does not discriminate between shells with or without *H. symbiolongicarpus* Weissberger 1995).

The only turbellarian associated with *P. longicarpus* is the polyclad *Stylochus zebra*, but it is much more commonly found in the lumen of shells inhabited by *P. pollicaris* (Lytwyn 1976, 1979; Lytwyn & McDermott 1976). Its rarity with *P. longicarpus* in the present study confirms that found previously in New Jersey by Lytwyn & McDermott (1976) and Lytwyn (1979). This polyclad has been recorded from three other species of hermit crabs from North Carolina [*Pagurus impressus* (Benedict), *Petrochirus diogenes* (Linnaeus) and *Dardanus venosus* (H. Milne Edwards)], all

with a lower prevalence than with *P. pollicaris* (Lytwyn 1979). It is an embryo predator of *P. pollicaris* (Lytwyn 1979), but also feeds on shell symbionts such as the white slipper limpet *Crepidula plana* (Lytwyn & McDermott 1976).

For many years the encrusting ctenostome bryozoan *Alcyonidium albescens* was known as *A. polyoum* (Hassall). However, Winston & Key (1999) have shown recently that the latter is a European species. *Alcyonidium albescens* is a common facultative inhabitant of the outer surfaces of *P. longicarpus*-inhabited *Nassarius obsoletus* shells, but is rarely associated with the shells of the living snail (Karlson & Cariolou 1982). It grows, however, on the shells of some other living snails and on shells occupied by *P. pollicaris,* as well as on brachyuran crabs and inanimate shell surfaces (Karlson & Cariolou 1982, Karlson & Shenk 1983, Key et al. 1999, McDermott pers. obs.). Buss & Yund (1988) found that it dominates *Hydractinia* spp. in competition for space on shells occupied by *P. longicarpus.*

The lumen of shells with *P. longicarpus* (and *P. pollicaris*) often contains the obligate polynoid polychaete symbiont, *Lepidonotus sublevis* Verrill (Pettibone 1963, Lytwyn 1979, Mercando 1983, McDermott pers. obs.). It was found in the lumen of approximately 25% of hermit crab shells in New Jersey (Table 3). This was about half of that recorded by Lytwyn (1979) in the 1970's from a much smaller sample. *Lepidonotus sublevis* was found to be 25 times more frequent in shells harboring male crabs, which may be related to crab size (males tend to be larger than females) rather than to sex per se (Mercando 1983). These scaled worms may occupy a considerable percentage of the shell's internal volume, and Mercando & Donaghy (1984) showed that *P. longicarpus* had more difficulty entering shells occupied by *L. sublevis*, i.e., they selected empty shells significantly more frequently than those with worms. Although Frotheringham (1976) demonstrated

that *L. sublevis* consumed detached embryos of *P. longicarpus* in the laboratory, there is still no evidence that the worm is an embryo predator under natural conditions.

Five species of gastropods are associated with *P. longicarpus* (Table 2). Of the three slipper limpets (Calyptraeidae), *Crepidula fornicata* (Linnaeus), *C. plana* Say and *C. convexa* Say, only the last two seem to show some predilection for inhabiting *P. longicarpus* shells (Table 3) (Karlson & Cariolou 1982, McDermott pers. obs.). *C. plana* lives on the inside of the shells, while *C. convexa* and *C. fornicata* are on the outside. The geographical distribution of *C. plana* is from New England to Georgia, and it is distinct from *C. depressa* Say, an inhabitant of hermit crab shells from Florida to Texas (Collin, 2000). *Crepidula plana* has a distinct relationship with crab-inhabited shells and is rarely detected on other substrates. This applies to shells inhabited by *P. longicarpus* (Shenk & Karlson 1986, Table 3), as well as *P. pollicaris* (Shenk & Karlson 1986, McGee & Targett 1989). Although the veligers of *C. plana* may settle and metamorphose on a variety of substrates, including the outside of hermit crab shells, they are usually found only on the inside of these shells where they are more protected from predation (Shenk & Karlson 1986, Collin 2000, present study). In this location, however, the limpet may be vulnerable to predation if the polyclad *Stylochus zebra* is present (Lytwyn & McDermott 1976, Lytwyn 1979). Effluents from *C. plana* and *P. pollicaris* in *Busycon carica* shells attract competent larvae to settle and metamorphose (McGee & Targett 1989).

The shell morphology of *C. convexa* living on hermit shells is markedly different in its dimensions than those on other substrates, i.e., the shells are shorter and narrower but greater in height (Franz & Hendler 1970). Unlike *C. fornicata* and *C. plana* which release veliger larvae, *C. convexa* has direct development and thus has a greater problem in distributing juveniles to

new locations. Attachment of *C. convexa* to the mobile hermit crab along with the high mobility of juvenile snails, however, aids in the colonization of new substrates (Hendler & Franz 1971). Thus, this association is a distinct benefit to *C. convexa* populations.

Two nudibranchs are associated with the gastropod shell of *P. longicarpus.* Strong evidence is presented here that the doridacean *Corambe obscura* has a very close association with one of its prey species, the encrusting bryozoan *Alcyonidium albescens.* Because of the possibility that some nudibranchs were dislodged from shells while being isolated in the field, it is likely that their 10.7% prevalence on the bryozoan is a minimal value. In Delaware Bay, New Jersey, Franz (1967) found that this nudibranch was always associated with, and fed on, the following encrusting bryozoans: *Alcyonidium verrilli* Osburn, *Conopeum tenuissimum* and *Membranipora tenuis* (Dudley (1973) clarified the identity of the last two species). *Corambe obscura* was also found with a *A. albescens* colony on a *Neverita duplicata* shell harboring *Pagurus pollicaris* from the same New Jersey location (McDermott, pers. obs.). Karlson & Shenk (1983) did not recover *C. obscura* from *A. albescens* colonies living on 39 shells of *Busycon carica* with *Pagurus pollicaris* and 18 live snails collected at the mouth of Delaware Bay. *Alcyonidium verrilli,* an upright species capable of forming large masses, has not been identified on shells with *P. longicarpus.* Cory (1967) found that *C. obscura* fed and deposited its egg strings on the colonies of *C. tenuissimum* and *M. tenuis* in the upper part of the Chesapeake Bay, Maryland. Wass (1972) reported that this snail is "often abundant on *Alcyonidium*" (presumably referring to *A. verrilli*) in the lower Chesapeake Bay, Virginia. Perron & Turner (1977) found the coiled egg strings of the snail on its cheilostome prey *C. tenuissimum,* and also noted that its larvae metamorphose on the colony. Perhaps an obligate metamorphosis may be involved in the *C. obscura–A. al-*

bescens relationship. The geographic distribution of *C. obscura* ranges in the Atlantic Ocean from the eastern United States to Brazil, and is found along the coast of northwestern Europe. It was introduced into the Black Sea in the late 1980's (Roginskaya & Grintsov 1990), and has been found subsequently in many locations within the Sea where it has apparently found encrusting bryozoans to sustain its reproduction (Roginskaya & Grintsov 1995, 1997).

Cuthona nana (Alder & Hancock) is a predator of *Hydractinia polyclina,* which is found primarily on shells inhabited by *Pagurus acadianus* in New England (Harris et al. 1975, Rivest 1978, Lambert 1991, Folino 1987, 1993, 1997). An unidentified species belonging to the same genus was found on *Hydractinia symbiolongicarpus* colonies on three shells of *Nassarius obsoletus* occupied by *P. longicarpus* in April and May 1986, from the same New Jersey location but not part of the collections in Table 3. Egg strings of the snail were on two of the shells, and on one shell with two nudibranchs most of the hydroid colony was destroyed. Lengths of the living nudibranchs were 3.5 mm for a juvenile and 10, 12 and 13 mm for adults.

Four shells among 2838 (0.1%) with living crabs had pycnogonids associated with colonies of *Hydractinia* (July and August 1987, May 1988). Three of the shells were *Nassarius trivittatus* and the other was *N. obsoletus.* The maximum number per shell was five (total = 10). These symbionts were juveniles and belonged to the genus *Anoplodactylus* (probably *A. lentus* Wilson). *Anoplodactylus lentus* is a common species along the eastern coast of the United States, living among and feeding on hydroids (Cole 1906, Sumner et al. 1913, Hedgpeth 1950).

Endolithic species (Tables 2, 3).—The shell-boring, spionid polychaete *Dipolydora commensalis* is an obligate commensal of gastropod shells occupied by hermit crabs including: *Pagurus annulipes* (Stimp-

son), *P. longicarpus, P. pollicaris* and *Clibanarius vittatus* Bosc (Andrews 1891, Hatfield 1965, Radashevsky 1989, Dauer 1991). It occurred in approximately 40% of the shells inhabited by *P. longicarpus* in this study, which compares well with the 36.8% prevalence (186 of 506) in five species of shells occupied by four species of hermit crabs, 91.8% of which were *P. longicarpus*, in Virginia (Dauer 1991). The other species of gastropod shells bored by *D. commensalis* from New Jersey were *Urosalpinx cinerea, Eupleura caudata, Neverita duplicata, Littoraria irrorata, Littorina littorea,* and *Busycotypus canaliculatus.* Hatfield (1965) recorded the worm from the shells of *Euspira heros* and *Buccinum undatum* Linnaeus. Although the prevalence of *D. commensalis* was significantly greater in the shells of *Nassarius trivittatus* than *N. obsoletus,* I have no rationale to explain this difference, except for possible dissimilarities in mineralization that may make the one shell more favorable for boring. The polychaete bores into the columella of shells producing a tube which in some cases eventually enters the lumen of the shell near the apex (Andrews 1891, Hatfield 1965, Radashevsky 1989, Dauer 1991, Williams 1995). The anterior end of the worm is usually located at the opening of the tube in the columella which is located on the medial side of the shell aperture. Here the worm extends its palps and draws food particles into the mouth (Dauer 1991, Williams & McDermott 1997). J. D. Williams (per. comm.) found that worms whose burrows reach the shell lumen, prey on the developing embryos attached to the pleopods of *P. longicarpus* in Rhode Island. Williams (1999, 2000, 2001) also reported that *Polydora* spp. and *Trypetesa* sp. inhabiting gastropod shells with hermit crabs from the Indo-West Pacific are also embryo predators, so that this may be a more common phenomenon than previously recognized. *Pagurus longicarpus* living in shells bored by *D. commensalis,* rather than normal shells, may be more vulnerable to predation because these shells are less resistant to crushing forces (Buckley & Ebersole 1994).

Other spionid polychaetes are boring facultative symbionts of shells inhabited by *P. longicarpus. Polydora websteri* Hartman was reported in shells from Maine (Blake & Evans 1973), and *P. neocaeca,* recently described by Williams & Radashevsky (1999), was recovered from shells in Rhode Island. Also in shells from this state was *Dipolydora socialis* (Schmarda) (Williams per. comm.). The superficial nature of the burrows of these species, however, suggests that they are not embryo predators.

The acrothoracican barnacle *Trypetesa lampas* burrows into gastropod shells occupied by hermit crabs (Tomlinson 1969a, 1969b), and was detected in approximately 5% of the 5041 shells examined in New Jersey. The significant difference in the prevalence of this barnacle between *Nassarius obsoletus* and *N. trivittatus* may be related to the larger size attained by the former, some difference in the calcereous composition of the shells, or the much greater abundance of *N. obsoletus* in the Hereford Inlet estuary. Barnacle burrows are detected only on the inner surfaces of the body whorl of cracked shells where slit-like openings allows the cirri to protrude into the lumen. Beyond this opening is the enlarged chamber harboring the barnacle. Other acrothoracican barnacles burrow into a variety of calcareous substrata (e.g., gastropod and bivalve shells, corals), but *T. lampas* is an obligate associate of hermit crabs. This association obviates harmful silting experienced by species living in uninhabited gastropod or bivalve shells (Tomlinson 1969a, 1969b). In New England waters, this barnacle is found in the shells of *Euspira heros* and *Neverita duplicatus* occupied by hermit crabs (Sumner et al. 1913, Zullo 1963). *Neverita duplicatus* shells inhabited by *Pagurus pollicaris* from New Jersey are also infested with *T. lampas* (McDermott pers. obs.). White (1969) found *T. lampas* in the shells of several spe-

cies of gastropods inhabited by *Pagurus bernhardus* (Linnaeus) in Wales. Some species of shells were heavily infested, e.g., 67.2% of 2249 *Buccinum undatum* Linnaeus shells were infested, and there were positive correlations between shell length and the prevalence and numbers per shell (White 1969).

Tomlinson (1969a) said that *T. lampas* "... in general does little if any harm to the host. All species of the order collect food without taking from or giving anything of value to the host," although the gastropod shell may be weakened by the presence of numerous barnacles. Recent studies by Williams (1999) may eventually modify Tomlinson's observations. He showed that a species of *Trypetesa* found in hermit crab shells from the Philippine Islands ingest crab embryos in nature.

Found on or in the crab (Tables 2, 3).— Two species of ciliated protozoans are ectosymbionts of *P. longicarpus.* One is the loricate peritrich *Lagenophrys eupagurus* Kellicott, 1893, (Lagenophryidae) that attaches to the crab's gills (Kellicott 1893, Clamp 1989, Fernandez-Leborans & Tato-Porto 2000). It is not specific for *P. longicarpus,* having been reported from thirteen other species of crustaceans, none of which was a hermit crab (Clamp 1989). Members of this genus are well-known as ectosymbionts of crustaceans. The gill filaments of hermits from New Jersey were not examined for this species. The unidentified ciliate (Table 2) is a heterotrichous folliculinid that was periodically found cemented to different parts of the crab's body and also on crab shells. The species appears to be a facultative commensal and is similar to *Platyfolliculina paguri* Andrews & Reinhard, 1943, which attaches to the body of *Pagurus pubescens* Kröyer, from the coast of Maine (Andrews & Reinhard 1943).

Plerocercoids of the tetraphyllidean cestode, *Calliobothrium verticillatum* (Rudolphi) are found in the tubules of the anterior midgut ceca of *Pagurus pollicaris* Say collected in the Woods Hole region of Massachusetts (Caira & Ruhnke 1991). Cherry et al. (1991) suggested that >95% of hermit crabs from this area were infected (it is not clear whether this value referred just to *P. pollicaris* or all three hermits from the region). Smolowitz et al. (1993) demonstrated in histological sections that these plerocercoids cause inflammation to the mid gut ceca of *Pagurus* spp. (*Pagurus acadianus, P. longicarpus* and *P. pollicaris*). Unfortunately, although 39 crabs were sectioned for study, the authors did not record the identity of the crabs (R. M. Smolowitz, pers. comm.). The adult parasite is found in the spiral valve of the smooth dogfish *Mustelus canis* (Mitchill) (Caira & Ruhnke 1991).

The occurrence of *Mytilus edulis* spat attached to the body of *P. longicarpus* on a seasonal basis is not unprecedented, because such was reported more than a half century ago from Woods Hole, Massachusetts by Andrews & Reinhard (1943).

Pagurus longicarpus serves as an intermediate host for the acanthocephalan *Polymorphus* sp. in the Woods Hole area (Reinhard 1944). Cystacanths were found in the abdominal cavity on the outer walls of the gut or among the tubules of the digestive gland. Usually there was only one cystacanth per host, and approximately one percent of the crabs were infected. These cysts are glistening white, have a mean length and width of 2.6 and 1.3 mm, and are easily seen through the thin abdominal wall (Reinhard 1944). During the course of the present study only a small but unrecorded percentage of the live crabs were dissected, and no cystacanths were found.

Pagurus longicarpus harbors three epicaridean isopod parasites, two belonging to the Bopyridae and the other to the Entoniscidae (McDermott 1998). One of the bopyrids, *Stegophryxus hyptius* Thompson (subfamily Althelginae), lives on the abdomen of the crab. At the beginning of the past century it had a prevalence of 1.5–4.0% in the Woods Hole region of Massachusetts (Thompson 1902), and at mid-century Reinhard (1943, 1949) found the iso-

pods in 1.25–1.5% of the crabs examined. During the last part of the century crabs from the waters of New Jersey had a prevalence of 0.15% (14 of 9111) (McDermott 1998). This parasite is found at least as far south as Georgia and has little host specificity, parasitizing at least seven other species of related hermits (Markham 1974, 1988). *Stegophryxus hyptius* does not produce any noticeable changes in primary or secondary (pleopods) sex characters in *P. longicarpus* (Thompson 1902, Reinhard et al. (1947).

The other bopyrid, *Asymmetrione desultor* Markham, 1975 (subfamily Pseudioninae), is found along the southeastern coast of the United States, inhabiting the branchial chambers of *P. longicarpus* (Markham 1975). This parasite has been found on five other species of hermits (Markham 1988), but it was not seen in the hermits from New Jersey.

The hemocoel-dwelling entoniscid *Paguritherium alatum* Reinhard, 1945, was recovered from 38 of 4600 (0.8%) hermits collected in 1943 in the Woods Hole area (Reinhard 1943, 1945). In 1946, Reinhard & Buckeridge (1950) collected ~100 infected *P. longicarpus* from the same locale, for the purpose of documenting the effect of the parasites on the secondary sex characters of the hosts, but prevalence was not recorded. Adkinson and Heard (1978) found the entoniscids in 3% of ~300 crabs that they examined in North Carolina. An alternate host for *P. alatum* in North Carolina is *Pagurus annulipes*; two of ~250 crabs were parasitized (Adkinson & Heard 1978). In New Jersey the prevalence of *P. alatum* was only 0.11% (4 of 3703). *Paguritherium alatum* castrates its female host and causes a pronounced reduction in the length of endopodal rami and a reduction of endopodal hairs (Reinhard & Buckeridge 1950); the parasitized male is not modified externally. Simultaneous parasitism in *P. longicarpus* with *P. alatum* and *Stegophryxus hyptius* occurs, but is rare (Reinhard & Buckeridge 1950).

Rhizocephalans have never been reported from *Pagurus longicarpus,* but its congener *P. pubescens* Kröyer, 1838, from the waters of Maine harbors *Peltogaster paguri* Rathke (prevalence up to 25%), which also parasitizes the European *P. bernhardus* (Reinhard 1939, 1942, Walker & Pearse 1939). *Pagurus acadianus* Benedict, from the same locality as *P. pubescens* is not parasitized by this barnacle.

Conclusion

Within this gastropod shell-*Pagurus longicarpus* complex are a number of biological relationships that deserve experimental study to further define their nature. This applies also to other species of hermit crabs whose associates are well known, e.g., the European *P. bernhardus* (Jensen & Bender 1973, Lancaster 1988). Such relationships involve a variety of predators and prey both on the outside and in the lumen of the shells, shell symbionts involved as crab embryo predators (a type of periodic parasitism involving only crabs of one sex), and host-parasite relationships involving the crabs as definitive or intermediate hosts. In all cases there is much to be learned about the factors involved in the establishment of all associates on and in the shell and with the crab itself. Just as the hermit crab is attracted to the physical nature of snail shells, so too is it likely that the associates may show preferences for attachment to shells with a particular topography or chemical composition. Likewise, predators are attracted by some means (e.g., chemical attraction) to certain prey species that precede them in their attachment to hermit crab shells.

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